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# Masticatory Apparatus in the Spectacled Bear *Tremarctos ornatus*

D. Dwight Davis
*Curator, Division of Vertebrate Anatomy*

The South American spectacled bear (*Tremarctos ornatus*) is unique among living bears in having a deep fossa on the body of the mandible immediately in front of the masseteric fossa. This depression is sometimes referred to as the "premasseteric fossa." A similar fossa was present in the extinct *Tremarctotherium* of the Pleistocene of North America, a related bear, and to a much lesser degree in the extinct *Arctotherium* of the Pleistocene of South America. *Tremarctos* is now confined to the Amazonian slopes of the Andes, but had a much wider range in the Pleistocene; fossil remains have been found as far north as Mexico and Florida (Stock, 1950). This is a typical relict distribution.

Little is known of the habits of *Tremarctos*. Cabrera and Yepes (1940) state that it is one of the most herbivorous of bears, feeding largely on the fruits and young leaves of certain palms. These authors say that in Ecuador it feeds on the "pambili" palm (probably some species of the tribe Iriarteineae), a tree that reaches a height of 24–30 meters. The bear climbs to the top of the tree and tears off whole branches, letting them fall to the ground and descending later to feed upon them. Its true home is in the virgin forest, where it passes a large part of its life in the crowns of the trees.

Two adult individuals in the Zoo in Brookfield, Illinois, are fed on the same diet as other bears in the Zoo, except that *Tremarctos* refuses fish. The diet consists of dehydrated dog food (16 per cent dry weight meat by-products) dampened with water, fresh vegetables, and fresh meat. According to Robert Bean, the Director of the Zoo, *Tremarctos* shows about the same interest in fresh meat as do black bears (*Ursus americanus*) and sloth bears (*Melursus ursinus*); it does not eat meat as readily as do grizzlies or polar bears.

The attendants at the Zoo state that they have never observed any indication of a functional cheek pouch in *Tremarctos*, nor have these bears been observed using a forefoot to force food from the cheek pouch into the mouth, as do monkeys and rodents that have cheek pouches. I observed these bears through 8× binoculars while they were eating various types of food and was unable to detect any differences between their masticatory behavior and that of other bears. Dog meal is licked from the ground and swallowed directly. Carrots and bananas are held between the apposed palms of the forefeet, the animal sitting on its haunches in a posture reminiscent of the giant panda during feeding, and pieces are bitten off the end and chewed up.

No one has examined the soft structures associated with the premasseteric fossa in *Tremarctos*, or attempted to explain their significance. Chicago Natural History Museum recently received the carcass of a specimen, an adult male, that died in the Brookfield Zoo. The head of this animal was embalmed and dissected. Three skulls of *Tremarctos*, two adults and a juvenile, were also available for comparison. Parallel dissections were made on the embalmed head of an adult male Tibetan bear (*Ursus tibetanus*), also from the Brookfield Zoo.

The drawings illustrating this report are the work of Miss Phyllis Wade. I have profited from numerous discussions with Dr. Harry Sicher, of the School of Dentistry, Loyola University, and Dr. E. L. DuBrul, of the College of Medicine, University of Illinois.

## THE SKULL

The premasseteric fossa is a large ovate depression in the lateral surface of the body of the mandible, immediately in front of the masseteric fossa (fig. 2). It lies below and behind the last molar tooth. The antero-posterior diameter of the fossa exceeds the vertical diameter, and the floor is a paper-thin area of the body that bulges mesad slightly on the lingual surface of the body. The lingual surface of the bulge is very smooth. The external face of the mylohyoid sheet lies directly against this convexity, and internal to this and pressed closely against it is the body of the tongue. Thus, when the tongue is extruded there is a double sliding contact; the mylohyoid slides forward over the smooth convexity of the mandible, while the tongue itself is sliding forward over the medial surface of the mylohyoid. This surface of the mandible is slightly concave in *Ursus* and is separated from the mylohyoid by fat.

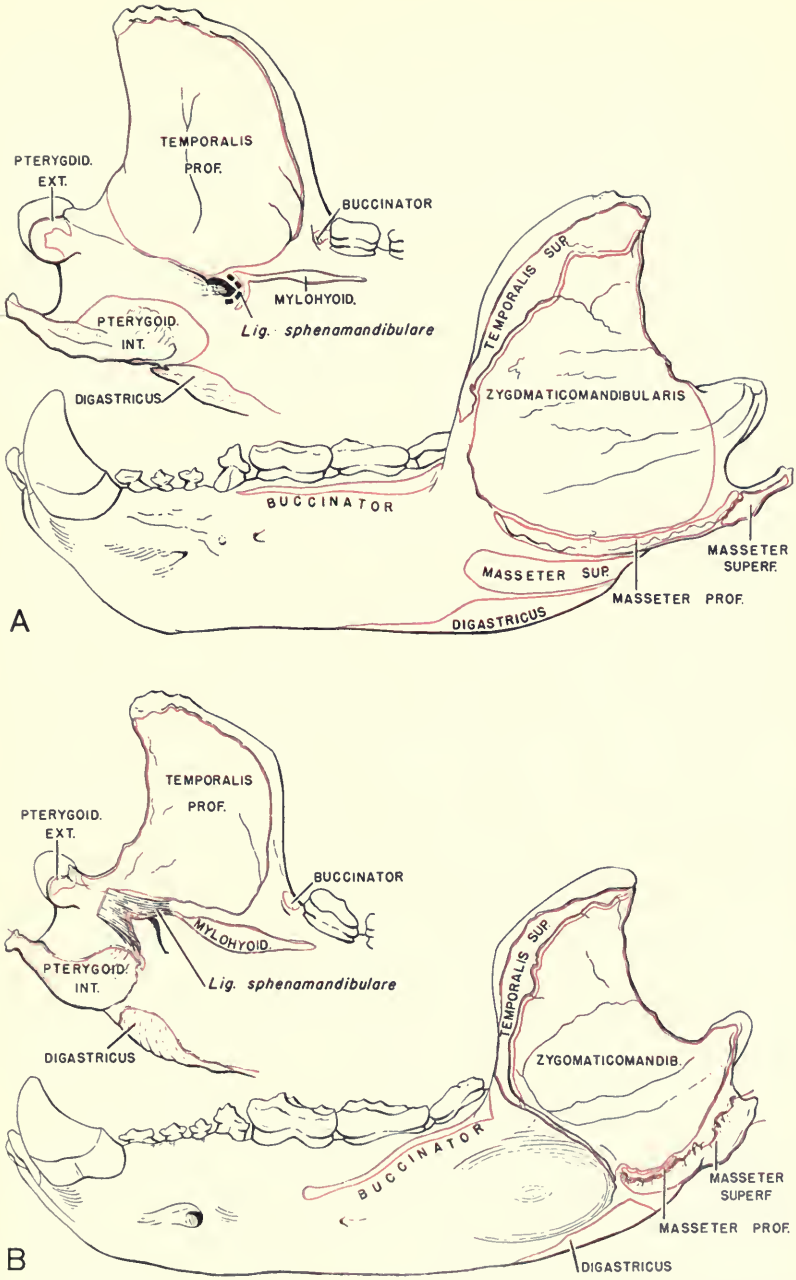


FIG. 2. Outer surface of mandible and inner surface of ramus of Tibetan bear (A) and spectacled bear (B) to show premasseteric fossa and areas of muscle attachment.

The alveolar canal passes through the dorsal wall of the fossa, in some specimens making a slight prominence in the fossa, and the root of the last lower molar lies above the canal. The entrance to the canal is laterally compressed instead of round as in *Ursus*, and it is bounded medially by a small lingula-like projection, which is not, however, associated with the attachment of the sphenomandibular ligament (fig. 2).

Directly below the fossa the inferior border of the ramus is of normal thickness. Thus the premasseteric fossa extends almost through the entire thickness of the body, but leaves intact the alveolar border of the body above it and the inferior border of the mandible below it.

The masseteric fossa differs considerably from that of *Ursus* (fig. 2). From the alveolar border the anterior edge of the fossa angles sharply backward and downward in a line that is slightly convex posteriorly. The anterior border of the fossa is elevated into a prominent wing-like ridge, 10–12 mm. high, that ends abruptly about 15 mm. above the inferior border of the mandible. The narrow inferior masseteric crest bounding the fossa below in *Ursus* is in *Tremarctos* a wide scar extending ventrad nearly to the inferior border of the mandible, which destroys the characteristic notch situated behind the marginal process in typical bears and eliminates the marginal process itself. The angular process is wider transversely than in *Ursus*. Thus the masseteric fossa, compared with that of *Ursus*, is much reduced anteriorly and slightly increased ventrally; its total area is relatively greatly reduced.

The coronoid process is rotated slightly forward on the ramus, as compared with that of *Ursus;* its posterior edge forms an angle of about 60° with the toothrow, compared with about 80° for *Ursus*. The axis of the masseter-temporalis insertion is thus rotated counterclockwise about 20° from that of *Ursus*. There are numerous prominent irregular ridges on its lateral surface, where the zygomatic part of the temporal muscle inserts.

The capitulum is more clearly divided into a lateral half facing dorsally and a medial half facing posteriorly than in *Ursus*. In one specimen of *Tremarctos* these two areas are separated by a shallow groove, and in an aged zoo animal they are divided by a deep constriction. The medial half, which would transmit a posterior thrust of the mandible, far exceeds the lateral half in diameter and area. The axis of the capitulum forms an angle of about 10° with the transverse axis of the skull; in *Ursus* this angle is only about 5°.

There are other differences in the skull associated with the differences in the posterior part of the mandible. The zygomatic breadth in *Tremarctos* is greater than in *Ursus*. The zygomatic arch is slightly more arched dorsally, and the posterior half of the arch is expanded vertically. The muzzle is relatively shorter in

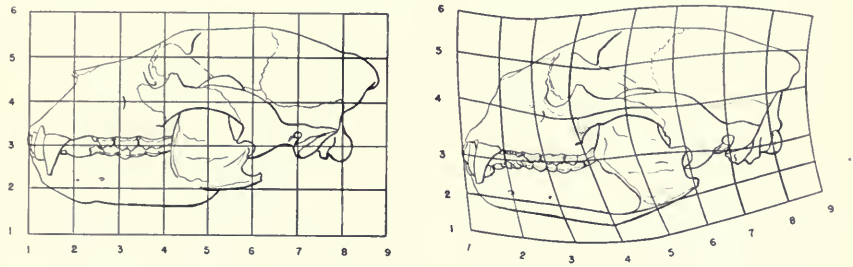

FIG. 3. Distortion grid for *Tremarctos ornatus* (right) based on *Ursus horribilis* (left).

*Tremarctos*. The frontal region of the skull is somewhat vaulted, and the mandible is deeper below $M_3$. The mandibular articulation is relatively higher above the level of the toothrow; as Arendsen de Wolff-Exalto (1951) has shown, this tends to distribute masticatory pressure over the toothrow. The cheek tooth series (P4–M2), reckoned against basal length of skull, is slightly longer than in *Ursus*, and $M^1$ (but not $M^2$) is relatively wider than in *Ursus*. The axis of $M_3$ is inclined upward at an angle of about 30°.

Most of these differences are relatively slight, and most of them are apparent in a distortion grid (fig. 3). Except for the premasseteric fossa, the features that distinguish the skull of *Tremarctos* from the skull of *Ursus*, although much less exaggerated, are similar to the features that distinguish the skull of the giant panda (*Ailuropoda*). *Ailuropoda* is the most herbivorous of living carnivores.

## TONGUE AND ORAL VESTIBULE

The tongue does not appear to differ significantly from the tongue of *Ursus*. In the fixed condition it is widest about 35 mm. back of the tip, with a spatulate tip occupying the space behind the incisors and the posterior border of the mandibular symphysis, and an enormous body twice as long as the free tip.

The lips are large and loose, as is characteristic of bears. The angle of the mouth is situated at the level of the fourth upper

premolar (the carnassial), as in other canoid carnivores. The outline of the oral vestibule, the part of the mouth cavity lying external to the teeth, is strikingly different from the vestibule of typical bears. In *Ursus* the vestibule is a narrow, nearly straight-sided tube leading from the anterior end of the mouth back to the space behind the

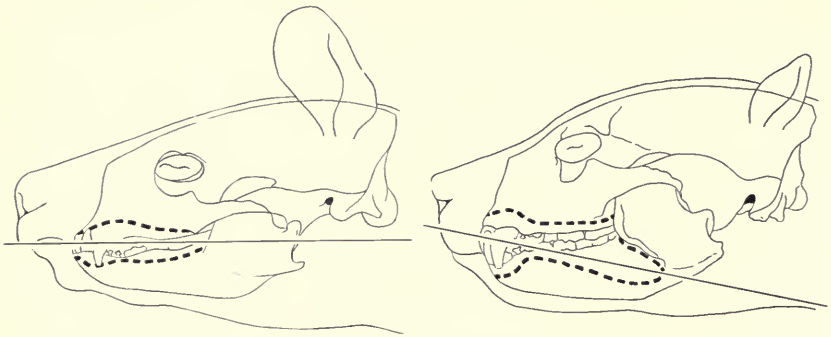

FIG. 4. Profile views of head of *Ursus tibetanus* (left) and *Tremarctos ornatus* (right), showing outlines of vestibulum oris.

last molar teeth; its axis is parallel to the occlusal plane. In *Tremarctos* the superior border of the vestibule resembles that of *Ursus*, but the inferior border slopes from the first lower premolar down to the inferior border of the premasseteric fossa, and the axis of the vestibule forms an angle of about 12° with the occlusal plane (fig. 4). Thus, the premasseteric fossa lodges a postero-ventral extension of the oral vestibule, with the axis of the vestibule shifted to lead directly into it. The mucous membrane lining the vestibule is unpigmented. It is relatively smooth except for a dense group of prominent papillae on the lining of the cheek immediately behind the corner of the mouth. A shallow pit in the inferior border of the vestibule at the level of the first lower molar marks the juncture between the orbicularis oris and buccinator muscles. The mucous lining of the posterior extension that fills the premasseteric fossa resembles the mucous membrane of the remainder of the vestibule, except that it has a slightly puckered appearance.

The postero-ventral extension of the oral vestibule is functionally a cheek pouch of very limited capacity, with a lateral wall capable of limited distension. The lateral wall is formed chiefly of the buccinator muscle, which in turn is overlain by the plate-like platysma. Food would inevitably enter this cavity during masti-

cation, and indeed the vestibule anterior to the cavity seems designed to promote the entrance of food into the cavity.

## VESSELS AND NERVES

The vessels and nerves in the cheek region (fig. 5) do not appear to differ significantly from the norm, except that division into superior and inferior labial branches is farther posterior. The external

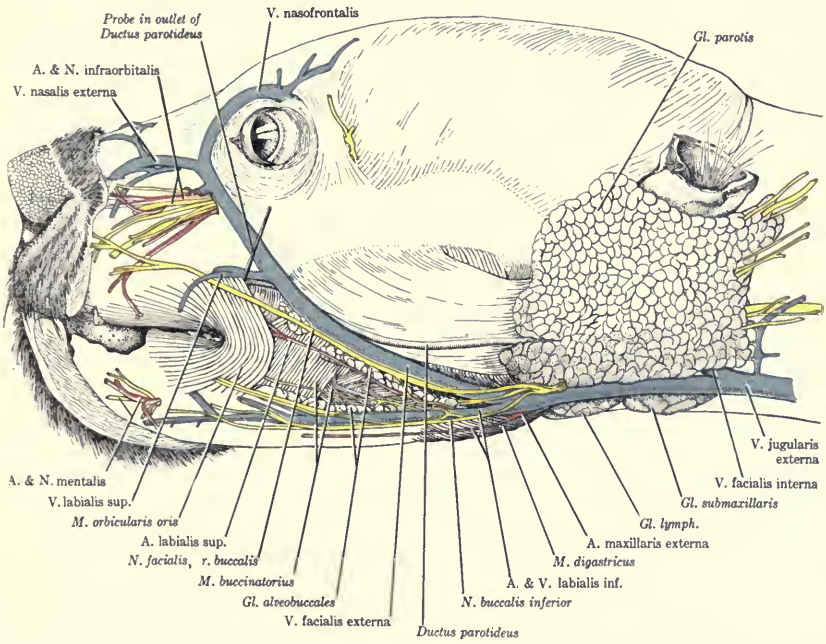


FIG. 5. Superficial dissection of head of *Tremarctos*. Most of the facial musculature has been removed. × ½.

maxillary artery and external facial vein run forward together along the inferior border of the masseteric fossa. The inferior labial artery and vein are much smaller than the superior labial artery and deep facial vein.

## SALIVARY GLANDS

The *parotid gland* is a large flattened structure lying below the ear and embracing the base of the ear cartilage. It is rectangular in outline, measuring 75 mm. in height by 60 mm. in width and

weighing 71 grams. Its anterior border overlaps about the posterior fifth of the masseter muscle, and its inferior border is on a line with the inferior border of the masseter, slightly overlapping the external facial vein from above. The gland completely surrounds the internal facial vein from the external jugular to the posterior border of the digastric. The parotid duct emerges well below the center of the gland and passes forward almost horizontally across the lower third of the masseter, terminating in the cheek near the gum line, opposite the middle of the first upper molar.

The *submaxillary gland* is a large compact pear-shaped structure lying below the parotid gland and covering the posterior part of the digastric muscle. The surface is smoother and less lobulated than that of the parotid gland. It measures 40 mm. in height by 32 mm. in antero-posterior diameter and weighs 17 grams. The submaxillary duct leaves the deep surface of the gland near its dorsal border, and runs forward between the masseter and the digastric, then forward between the mylohyoid and the root of the tongue to the symphysis, where it opens.

A large disk-shaped lymph gland, 35 mm. in diameter, lies immediately in front of the submaxillary gland.

The *sublingual gland* is an elongate flattened gland, triangular in cross section, situated on the medial side of the mandible at the posterior angle. The gland is 42 mm. long and 19 mm. in greatest width and weighs 1.5 grams. The posterior third lies in the sulcus between the internal pterygoid and digastric muscles; the anterior two thirds lies between the deep surface of the mylohyoid and the root of the tongue. Throughout its length the gland lies on the submaxillary duct.

There are numerous, somewhat scattered *alveobuccal glands* lying against the outer surface of the buccinator in the angle between the external facial and inferior labial veins. These extend forward to the angle of the mouth. They open into the mouth by numerous small ducts, which penetrate the buccinator.

## MUSCLES

Only the masticatory muscles, and the elements of the facial musculature that appeared to be related to the vestibulum oris, were considered.

The anterior part of the *platysma* is a wide, thin sheet completely covering the buccal part of the vestibulum oris. It is wholly super-

ficial to the buccinator. A typical *orbicularis oris* embraces the angle of the mouth, extending forward to the level of the canines above and below. Its posterior edge overlies the anterior edge of the buccinator, but the two muscles are readily separable.

The *buccinatorius*, which is the foundation of the true cheek, is an extensive sheet of nearly parallel vertical fibers. Anteriorly the fibers run almost directly from their origin on the skull to their insertion on the mandible. Farther posteriorly the superior end of the sheet is closely applied first to the anterior surface of the masseter, then to the winglike ridge forming the anterior border of the masseteric fossa, before it reflects into the wall of the cheek. The inferior end of the buccinator sheet lies against the ramus of the mandible, the fibers descending vertically and attached to the bone by loose areolar tissue, before the muscle is reflected dorsad to enter the wall of the cheek. The amount of the buccinator so attached to the mandible becomes increasingly greater as the premasseteric fossa is approached. Posteriorly the buccinator balloons out into a sac-like pocket that completely fills the premasseteric fossa; the muscle is loosely attached to the surface of the fossa by areolar tissue.

Dorsally the buccinator is attached to the maxilla along a line beginning at the root of the zygoma and running caudad above $M^2$. Behind $M_1$ the buccinator fibers pass through into the pterygoid fossa and attach to a tendinous aponeurosis on the medial surface of the internal pterygoid muscle. Inferiorly, attachment is to the mandible along a diagonal line beginning at the posterior end of $M_3$ and descending obliquely over the outer surface of the mandible to end at the level of the middle of $M_1$, just above the middle of the mandible.

The buccinator thus forms the foundation of the whole posterior part of the oral vestibule, which is functionally a cheek pouch. The pouch is strapped down by the platysma, which completely covers it externally. This condition is very different from that of the cheek pouch of the cercopithecid monkeys, in which the pouch breaks through the platysma, and in which the distensibility of the pouch is limited only by the buccinator fibers in its wall.

*M. temporalis* does not differ significantly from that of *Ursus*, except that it is relatively larger. It is divided into the usual superficial and deep parts by a heavy tendinous plane that arises from the superior and anterior edge of the coronoid process and extends nearly to the sagittal crest. Muscle fibers arise from both surfaces

of this tendinous plane, from the entire surface of the temporal fossa, from the deep surface of the temporal fascia that covers the muscle externally, and from the superior border of the posterior half of the zygomatic arch.

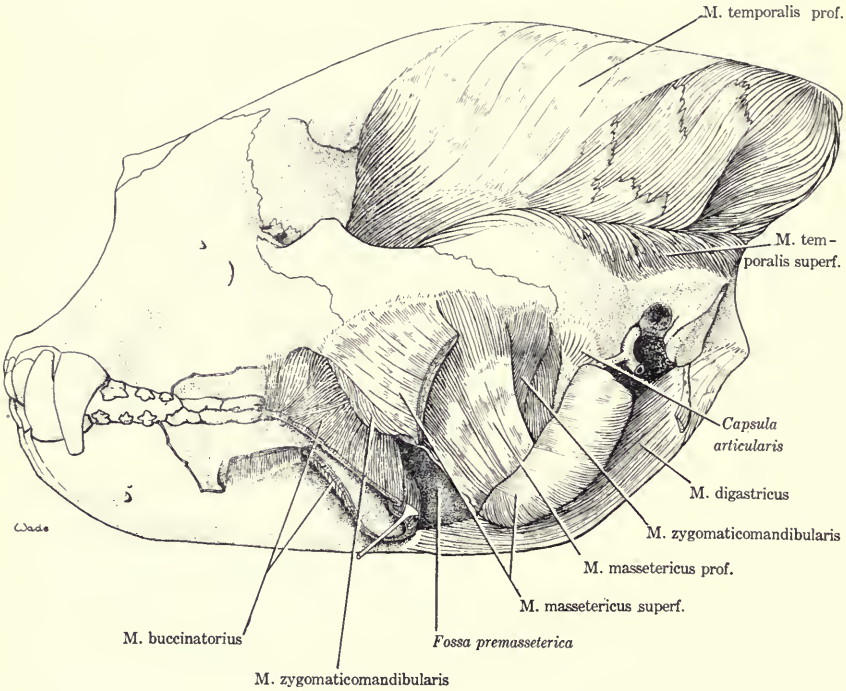


FIG. 6. Masticatory musculature of *Tremarctos*. The cheek pouch has been opened by a cut continuing caudad from the corner of the mouth, and the buccinator has been pulled forward and downward out of the premasseteric fossa. × ½.

The parts of the temporal muscle are distinct from each other and from surrounding muscles only near their insertions; near their origins there is much fusion. The *superficial temporal* arises chiefly from the deep surface of the temporal fascia and from the outer surface of the tendinous plane, with a few of the posteriormost fibers taking origin from the bony shelf above the auditory meatus and from the dorsal edge of the zygomatic arch forward to its middle. The superficial temporal inserts into a narrow area along the anterior and superior edge of the external surface of the coronoid process (fig. 2). The *deep temporal* arises from the deep surface of the ten-

dinous plane and from the entire surface of the temporal fossa, and inserts into the entire internal surface of the coronoid process.

*M. zygomaticomandibularis* is relatively large, and is more distinct from the temporal than in *Ursus*. The muscle is exposed on either side of the superficial masseter. It arises from the entire internal face of the zygomatic arch, including the dorsal surface of the posterior root of the arch. The anteriormost fibers continue the origin of the muscle down onto the deep surface of the heavy tendon by which the superficial masseter arises. This origin from the deep surface of the tendon continues almost without boundary into the adjacent anterior fibers of the deep masseter. The masseteric nerve divides the zygomaticomandibularis into the usual anterior and posterior parts, although these are otherwise poorly marked. Insertion is into the whole external surface of the mandible behind the premasseteric fossa, except for the small areas occupied by the superficial temporal and the masseter (fig. 2). The anteriormost fibers of the anterior division (including those arising from the masseteric tendon) insert into the prominent ridge that bounds the premasseteric fossa posteriorly.

The fiber direction of the zygomaticomandibularis is downward, mesad, and slightly forward. With the mandible closed, the dorsalmost fibers run nearly horizontally from the zygomatic arch to the coronoid process, the posteriormost fibers forming an angle of only about 7° with the horizontal. The deepest fibers run nearly vertically. As the mandible is opened, the originally horizontal dorsal fibers assume an increasingly vertical (and anterior) direction (fig. 7).

The mechanics of the zygomaticomandibularis is very complex, although the muscle itself is quite simple. The ventral fibers are functionally associated with the masseter in raising the mandible, in all positions of the mandible. The dorsal fibers, with the jaw closed or nearly so, are functionally associated with the external pterygoid of the opposite side of the head in shifting the mandible laterally. With the jaws open, these same dorsal fibers are functionally associated with the posterior temporal fibers in pulling upward and backward on the coronoid process.

*M. masseter* is divisible into the usual superficial and deep divisions. These are readily separable posteriorly, but the anterior fibers, especially near their origin from the zygomatic arch, cannot be separated.

The *superficial layer* is a dumbbell-shaped layer, 10 mm. thick, that covers all except a very small part of the deeper layer. It

also leaves a small part of the zygomaticomandibularis exposed anteriorly. The surface of the superficial layer is covered with a heavy tendinous aponeurosis except for a strip along the anteroventral edge of the extreme posterior end. The aponeurosis arises from the anterior half of the inferior surface of the zygomatic arch,

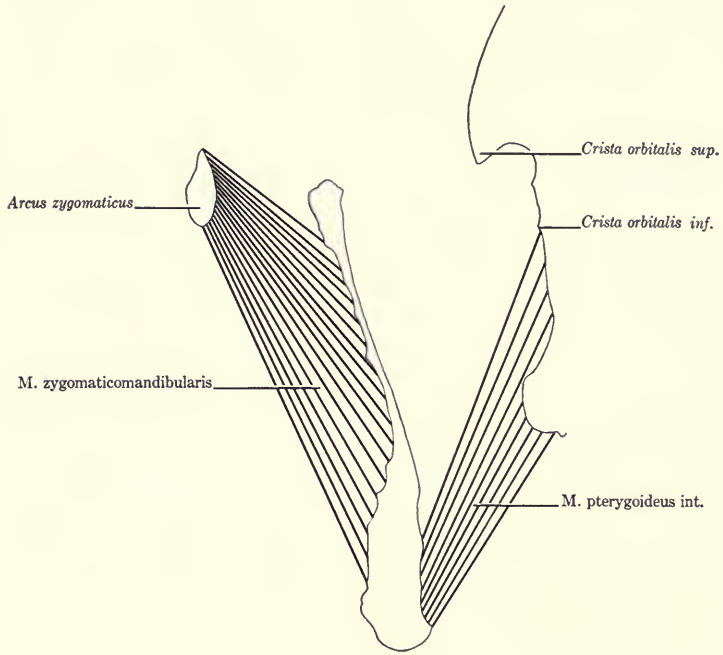


FIG. 7. Frontal section through skull of *Tremarctos* at level of coronoid process; teeth in occlusion. To show relations of zygomaticomandibularis and internal pterygoid muscles. The dorsal fibers of the zygomaticomandibularis run more nearly horizontally posterior to the level of the cut. Semidiagrammatic; × 1.

and the muscle fibers of the superficial masseter arise from the deep surface of this aponeurosis. There is a much thinner aponeurosis on the deep surface of the muscle. Most of the superficial layer inserts fleshily into the prominent scar directly beneath the masseteric fossa, on the lateral and inferior surfaces of the ramus and the angular process. Behind the angular process insertion is continued into a raphe formed with the internal pterygoid, which beyond the posterior border of these muscles is continued as a ligament that attaches to the inferior surface of the auditory meatus.

With the jaws closed, the fibers of the superficial layer form an angle, open anteriorly, of about 20° with the long axis of the toothrow.

The *deep layer* of the masseter, the smallest element of the masseter complex, is a thin muscle sheet, mostly covered with glistening tendon fibers on its superficial surface except near its origin. It leaves a small part of the zygomaticomandibularis exposed posteriorly. Origin is by fleshy fibers from the anterior two thirds of the inferior surface of the zygomatic arch, and insertion is by mingled fleshy and tendon fibers into a narrow line below the masseteric fossa, directly above the insertion of the superficial masseter. This division of the masseter has no attachment to the crest forming the anterior border of the masseteric fossa. The fibers of this layer form an angle, open anteriorly, of 65° with the long axis of the toothrow.

*M. pterygoideus internus* greatly exceeds the externus in volume. It is a fan-shaped muscle extending from the surface of the infratemporal fossa ventrad and slightly caudad to the posterior angle of the mandible. The extensive origin covers most of the infratemporal fossa, beginning anteriorly at the level of the sphenopalatine and pterygopalatine foramina. Origin (fig. 8) extends dorsally to the infraorbital crest and ventrally to the inferior edge of the pterygoid plate. Behind the level of the optic foramen the origin is continued posteriorly along a narrow line wedged in between the origin of the external pterygoid and the tensor tympani. Insertion is into the usual prominent scar on the medial surface of the angle of the mandible, extending posteriorly across the medial surface of the angular process. Behind the angular process insertion is continued into a raphe formed with the superficial masseter.

With the jaws closed, the fibers of the internal pterygoid form an angle of about 30° with the horizontal in the frontal plane, while in ventral view the angle varies from about 45° to 0° with the transverse axis.

*M. pterygoideus externus* is a very short cylindrical muscle extending from the posterior part of the infratemporal fossa to the medial end of the capitulum. Its fiber direction is almost transverse. Origin is from the posterior part of the infratemporal fossa, directly below the orbital fissure, where the muscle is wedged in between the internal pterygoid anteriorly and inferiorly, and the inferior surface of the temporal above. Seen from below, the muscle is divided into four distinct parts. The first three are cone-shaped,

with the apex of each cone forming a stout tendon. The tendinous apices point in opposite directions, interdigitating with each other, the most anterior attaching to the pterygoid plate, the second to the mandible, and the third to the pterygoid plate again. The general area of insertion is, as usual, into the medial end of the capitulum. The fourth and posteriormost division of the external

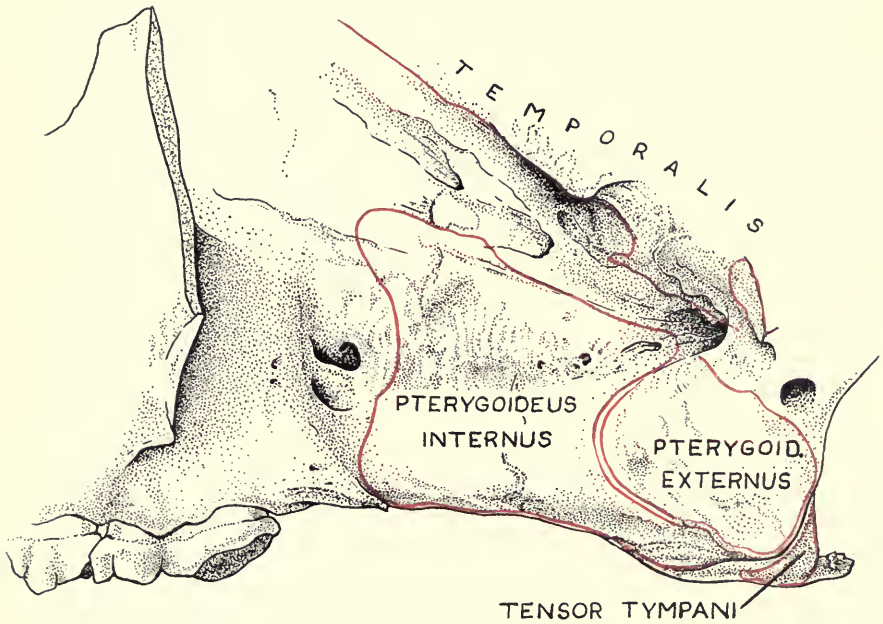


FIG. 8. Left infratemporal fossa of *Tremarctos*, showing muscle attachments.

pterygoid inserts into the medial end of the joint capsule and acts as a tensor of the capsule; since the disk attaches directly to the capsule, it would also tense and stabilize the disk.

*M. digastricus* arises from the paroccipital process and from the ridge connecting this with the mastoid process. It runs almost straight forward, closely applied to the inferior surface of the internal pterygoid muscle, and inserts into the inferior and adjacent medial surfaces of the mandible, from the level of the marginal process forward to the middle of the body of the mandible.

### THE MANDIBULAR ARTICULATION

The mandibular joint does not differ greatly from that of *Ursus*. The articular capsule is a tight sac attached above to the margin

of the mandibular fossa all around, and below to the neck of the condyloid process at the margin of the articular surface. At the lateral and medial ends the capsule is considerably thickened; the lateral thickening corresponds to the temporomandibular ligament of human anatomy. The posteriormost division of the external pterygoid muscle attaches to the medial end of the capsule.

The articular disk is a thin plate, firmly attached to the articular capsule throughout its entire circumference. It is thinner at the center than at the periphery but is much thicker posteriorly, where it rides against the postglenoid process. There is a large central perforation, in the form of an antero-posterior oval, midway between the lateral and medial ends of the disk. The external pterygoid muscle has no direct attachment to the disk. The disk is more tightly attached to the fossa than to the condyle, so that movement in the joint is largely between the condyle and the disk.

Two ligaments are associated with the mandibular joint. The *sphenomandibular ligament* is a stout flat band attached anteriorly to the mandible at the entrance to the mandibular foramen. It has two points of attachment, one above the foramen and the other below and slightly behind it. The attachment of the ligament thus bridges over the vessels and nerve that enter the foramen. The ligament extends posteriorly and slightly medially, to attach posteriorly to the anterior edge of the bulla just laterad of the canalis chordae tympani; there is usually a ridge or an anteriorly directed spine at its point of attachment. This ligament is taut when the jaw is closed. Some of the posterior fibers of the mylohyoid arise from it. In *Ursus* the sphenomandibular ligament is much more slender than in *Tremarctos*, but has similar relations.

The second ligament, which I propose to call the *petromandibular ligament*, is more slender. It attaches anteriorly to the medial surface of the capitulum, immediately below the inferior border of the external pterygoid insertion. Extending posteriorly and slightly medially across the medial end of the articulation, the ligament attaches posteriorly to the anterior edge of the bulla, anterior to and slightly mesad of the attachment of the sphenomandibular ligament.

*Joint movements.*—The only movements permitted in the mandibular joint of the bear are vertical rotation (hinge movement) and transverse gliding. These may, of course, be combined to produce what Sicher has called a "screw movement," and this is apparently the masticatory movement in all carnivores, whether merely

for cutting (as in cats) or for grinding (as in bears). Amplitude of lateral shifting is severely restricted anteriorly by the interlocking canines. Posteriorly, at the mandibular articulation, there is no such restriction. Manipulation of the mandible on the dry skull shows that there is considerable lateral shifting at the condyle, but almost none at the level of the incisors, that is, that the mandible rotates around a vertical axis lying a short distance in front of the incisors. This movement is facilitated by the fact that the mandibular articulations are not transverse, but their inner poles are inclined posteriorly; they form segments of the circumference of the circle of horizontal rotation. It is obvious that the maximum lateral movement in the dentition is at the level of the posteriormost molars.

The articular disk compensates for the incongruities of the joint surfaces and provides the surface against which the capitulum moves. It apparently does not move appreciably with relation to the mandibular fossa. The thickenings of the lateral and medial ends of the capsule restrict the horizontal excursions of the capitulum. The most important limitation to medial excursion, however, is the petrotympanic ligament. As can easily be demonstrated on a dissection, this ligament tightens as the capitulum moves medially, and soon impedes further medial movement; it functions exactly like the rope across the deck of an aircraft carrier, which brakes a landing plane by catching and holding it. The petrotympanic ligament prevents damage by the medial end of the capitulum to the mandibular nerve as it emerges from the foramen ovale, and to the internal maxillary artery. On the other hand, there is no apparent function performed by the sphenomandibular ligament.

## JAW MECHANICS

*Tremarctos vs. Ursus.*—The vertebrate jaw is customarily regarded as a Class III lever. This is true only where the coronoid process is not appreciably higher than the capitulum, as it is, for example, in man. Mechanically this is a remarkably poor arrangement for masticatory purposes; force is sacrificed to gain speed, and the useless force exerted at the mandibular articulation exceeds the useful force at the dentition. In carnivores the lever arm between the insertion of the masticatory muscles and the functional cheek tooth ($M_1$ or $M_2$) is about twice as long as the lever arm between muscle insertion and articulation. Therefore, to exert a force of 10 g. on the tooth, a force of $2 + 10 = 20$ g. would be exerted on

the joint; and, by the general law of the lever, a force of 10+20=30 g. would be required of the masticatory muscles (fig. 9).

The feeble human masticatory muscles are known to be able to develop a force of 7.2 kg. at $M_1$ (Howell and Brudevold, 1950). The enormous masticatory muscles of the Carnivora must be able to exert tremendous pressure between the cheek teeth, and if the

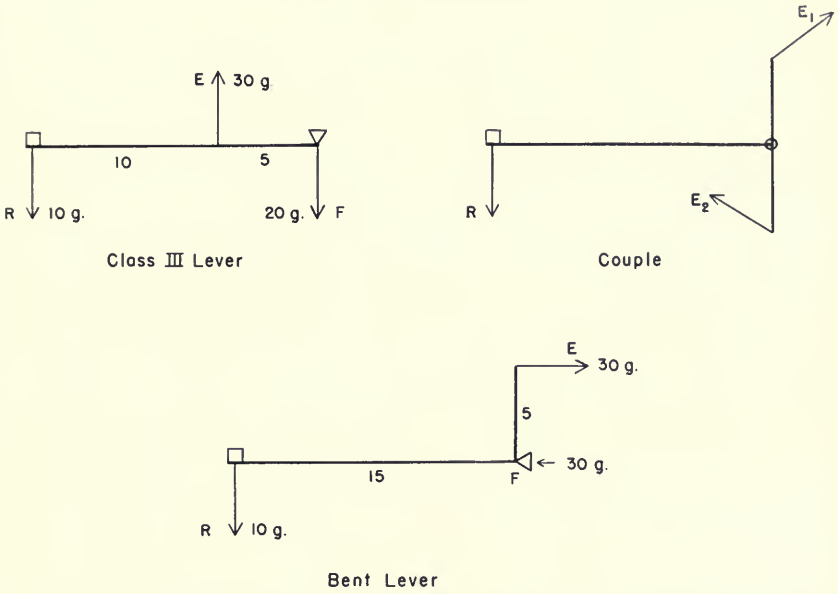


FIG. 9. Types of lever in mammalian jaw apparatus. R=resistance (useful force exerted at dentition); E=effort exerted by masticatory muscles; F=force at fulcrum (mandibular articulation).

jaw operated as a Class III lever this force would be approximately doubled at the articulation. Despite the buttressing of the joint by the zygomatic arch, it is unlikely that the bone could withstand forces of such magnitude.

In the Carnivora the coronoid process is higher than the articulation; the entire insertion of the temporal is at or above the level of the joint, and the insertion of the masseter below the joint. The fibers of the temporal slope upward and backward, the posteriormost being completely horizontal. The fibers of the masseter slope upward and forward. The fiber directions of temporal and masseter are approximately at a right angle to each other, and the result of their combined action would be to rotate the mandible around the

articulation as an axis. In other words, these two muscles form a *couple* acting like the arms of a driver on the steering wheel of an automobile (fig. 9). The advantage of the couple over the lever is that, disregarding torsion, *the forces acting at the fulcrum are reduced to zero.* Actually, as shown in the accompanying table, the mass of the temporal greatly exceeds the total mass of the masseter. To the extent that the force exerted by the temporal exceeds the force exerted by the masseter, the system functions as a *bent lever*, acting like a claw hammer when it is used to draw a nail (fig. 9). This is a modified Class I lever, and in this instance gives better mechanical advantage than a Class III lever. It has the disadvantage that the force at the fulcrum equals the combined forces of effort plus resistance. The force at the fulcrum is opposite in direction to the effort force (temporal muscle), and pressure would therefore be against the rear of the mandibular fossa. This process explains the tremendous development of the postglenoid process in carnivores.

TABLE 1.—RELATIVE WEIGHTS OF MASTICATORY MUSCLES IN CARNIVORES

| | *Tremarctos ornatus* | | *Ursus americanus*[1] | *Canis familiaris* | *Panthera onca* |
|---|---|---|---|---|---|
| | Weight in gms. | % | % | % | % |
| Masseter superf. | 19.5[2] | 7.5 | 11 | 15 | 21 |
| Masseter prof. | 7 | 2.5 | 3 | 3 | 2.5 |
| Zygomaticomand. | 36 | 14 | 11 | 6 | 2.5 |
| Temporalis | 151 | 58 | 58 | 58 | 59 |
| Pterygoideus int. | 17 | 7 | 5 | 7.5 | 6.5 |
| Pterygoideus ext. | 2.5 | 1 | 1 | 0.5 | 0.5 |
| Digastric | 26 | 10 | 11 | 9.5 | 8 |
| | 259.0 | 100 | 100 | 99.5 | 100 |

[1] Figures from Starck (1935). Starck's "Masseter III" is here regarded as a part of the zygomaticomandibularis.

[2] Heavy tendon removed.

The zygomaticomandibularis and internal pterygoid muscles form a sling for the mandible (fig. 7). Their combined action would elevate the mandible. The zygomaticomandibularis, acting with the external and internal pterygoids of the *opposite* side, would shift the mandible laterally toward the side on which the contracting zygomaticomandibularis is located.

Thus *elevation* of the mandible is accomplished by (1) the temporal-masseter couple, (2) the temporal alone acting as a bent lever, and (3) the zygomaticomandibularis-internal pterygoid sling.

*Lateral shifting* of the mandible is accomplished chiefly by the external pterygoid of the side opposite the shift, assisted by the internal pterygoid of this side and the zygomaticomandibularis of the side toward which the mandible is shifting.

The figures in Table 1 show an astonishing constancy in the relative mass of the temporal among carnivores, regardless of food habits. The pterygoids and deep masseter also show no significant variation. On the contrary, the superficial masseter and zygomaticomandibularis do vary significantly; their masses are, in fact, roughly in inverse ratio to each other. A large superficial masseter is associated with carnivorous habits, a large zygomaticomandibularis with herbivorous habits.

In *Tremarctos* the zygomaticomandibularis is relatively larger and the superficial masseter relatively smaller than in any other carnivore studied. The disproportion is significantly greater than in *Ursus*, where it already exceeds that for the flesh-eating carnivores. This is, moreover, the only feature in which the relative masses of the masticatory muscles of the bears differ significantly from those of the flesh-eating dogs and cats. The zygomaticomandibularis is, therefore, the key to the ursid modification of the primary carnivore masticatory musculature. Its relatively greater mass in *Tremarctos* is correlated with the more herbivorous diet of this bear.

Is the premasseteric fossa of *Tremarctos* correlated with the increased size of the zygomaticomandibularis, or is it associated with a functional cheek pouch that plays a significant role in the feeding habits of this animal?

A cheek pouch, developed in the buccinator muscle as in certain rodents and primates, is indeed present in *Tremarctos*, and it is lodged in the premasseteric fossa. But everything argues against its being a functional structure. It is scarcely capable of containing a golf ball, and so is ridiculously small for the size and food requirements of the animal. And a functional pouch occurs elsewhere only in social animals that compete for food (primates), or in animals that forage for food and retreat to a safe place to masticate it (rodents). Bears fall into neither of these categories. It seems likely that the buccinator muscle has merely expanded posteriorly to occupy an area vacated by the retreating masticatory muscles, and in so doing has adapted itself to the modeling of this region.

Then why does a depression, the premasseteric fossa, develop in the body of the mandible, in the area from which the masseter and zygomaticomandibularis have retreated? A similar fossa was

present in dogs of the subfamily Amphicynodontinae (illustrations of *Hemicyon* and *Dinocyon* in Frick, 1926), associated with typical sectorial cheek teeth. There is a tremendous fossa with a paper-thin floor in the body of the mandible in the mandrill (*Papio maimon*), situated immediately behind the root of the canine and therefore anterior to the level of the ramus and of the cheek pouch.

It is significant that these fossae are so situated that they do not impair the structural integrity of the mandible. Starck (1935) determined the trajectory systems in the skull of the domestic cat and the Tibetan bear by means of X-rays and the "split-line" method of Benninghoff. In the carnivore mandible a main basal trajectory runs between the capitulum and the canine tooth, extending in an arch along the lower edge of the mandible. This part of the mandible remains intact; the premasseteric fossa never encroaches on it. A second trajectory, the coronoid trajectory, follows the anterior border of the coronoid process, which is thickened and continues directly into the body of the mandible above the premasseteric fossa. Alveolar trajectories connect the alveoli of the cheek teeth with the basal trajectory in front of the fossa; in the mandrill the alveolar trajectory is a dorsally convex arch sitting on the basal arch and embracing the fossa. Thus, in the bears, the dogs, and the mandrill the fossa is situated in tissue that contributes little or nothing to the internal support of the mandible. From the architectural standpoint the bone that has been removed is "excess."

The presence of mandibular fossae in forms as widely separated in masticatory behavior as the mandrill, the dogs, and the bears suggests that it merely reflects some obscure feature of mandibular architecture that I, at least, am not competent to analyze. In *Tremarctos*, I believe, it is the mechanics of the zygomaticomandibular muscle that is responsible, but I am unable to demonstrate this. That it is not of necessity associated with secondary herbivory in carnivores is shown by the giant panda (*Ailuropoda*), which has no suggestion of a premasseteric fossa. Presumably other causes would be involved in the extinct dogs, with their sectorial dentition, since the zygomaticomandibular is relatively small in living dogs. Certainly the cause for the fossa of the mandrill would be quite different from that for either group of carnivores.

## SUMMARY

1. There is a deep premasseteric fossa on the body of the mandible in *Tremarctos*. A similar fossa was present in certain

extinct bears and in extinct dogs of the subfamily Amphicynodontinae.

2. In *Tremarctos* the fossa lodges a pouch-like posterior extension of the oral vestibule, which is supported by the buccinator muscle.

3. The morphology of the head in *Tremarctos*, compared with *Ursus*, is adapted for increased herbivory of the masticatory function. Particularly notable is the decreased mass of the superficial masseter and the increased mass of the zygomaticomandibularis.

4. What is known of the natural diet of *Tremarctos* indicates herbivorous habits. In captivity its diet is similar to that of other bears.

5. It is suggested that fossae in the body of the mandible reflect obscure forces modeling the mandible. The basic architectural integrity of the mandible is not impaired, in any of the forms studied, by the presence of a fossa.

6. It is suggested that the zygomaticomandibular muscle is involved in the development of the fossa in *Tremarctos*, and that other factors determine its presence in dogs and baboons.

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